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ORIGIN, DISPERSAL, AND VARIABILITY OF THE LIMA BEAN, PHASEOLUS LUNATUS[1]

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ORIGIN AND DISPERSAL

COLUMBUS on his first voyage of discovery found beans under intensive cultivation by the Indians in Cuba. Other early Spanish explorers likewise encountered cultivated beans. English and French explorers, following the Spanish, found beans along the whole Atlantic Coast as far north as Virginia (*10*).[3] The lima bean, however, appeared to be restricted to the area south of the Potomac River in Virginia, where it is still found in close resemblance to the original primitive forms of the inhabited islands of the West Indies, Brazil, Colombia, Peru, Central America, the western coast of Mexico, and northward to the Hopi pueblos in the southwestern United States. The antiquity of these lima beans is further confirmed by the extensive discoveries of large lima beans of various colors in the tombs of ancient Peruvian cultures (*49*) and in excavations of pre-Columbian ruins of the southwestern agricultural Indians (*38*).

It is evident from the records of explorers and botanists that the lima beans have been distributed by man. From these early bean cultures, the lima beans have escaped into the jungles and have established themselves in a wild state where they are recovered at the present time. In North and South America these escaped lima beans are undoubtedly of pre-Columbian origin, but similar escapes are found throughout the world in tropical countries where they have been introduced in post-Columbian times (*43*).

The origin of the lima bean has been confused. The origin of the large lima has been placed in the Amazon Valley by Bentham (*6*) and accepted by deCandolle (*9*) in his studies on the origin of cultivated plants. The small-sized lima beans have been given various origins in the West In-

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[3] Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

dies and Central America. It is the intention of this study to definitely place the origin of the lima bean and to define the route of distribution especially in pre-Columbian times.

DeCandolle (*9*), the outstanding authority on the origin of cultivated plants, believed the origin of a cultivated plant could be determined by the discovery of wild progenitors, but unfortunately for this concept some cultivated crops like maize and the common bean (*Phaseolus vulgaris*) have not yielded wild progenitors. Such plants may not have wild progenitors because they may have originated in accidental hybrids which were seized upon and cultivated and improved by primitive agriculturists. The survival of such hybrids may not have been possible in an uncultivated state, a theory accounting for their disappearance. Continued selection under cultivation would tend to produce plants so different as to render identification of relationships doubtful or impossible.

The difficulty of finding a wild progenitor for the cultivated plant was greatly reduced by Vavilov (*44*), who, aware of this condition, believed that the origin of a cultivated plant could be placed by the concentration of species where only wild forms existed or by the increase in the number of cultivated forms towards the center of origin. He employed, in further defining the origins, the specificity of fungus and insect pests, as well as archaeology. Both the concept of deCandolle and that of Vavilov were successfully employed in the placing of the origin of the lima bean, as will be shown in the evidence to follow.

In a search for the origin of the lima bean, the records of ancient beans found in Peru (*49*) and in various parts of the southwestern United States (*38*) were studied. This material, however, was limited and frequently unsatisfactory. It followed, therefore, that the genetic evidence presented by the living material found wild or in cultivation would be of definite assistance. In a search for material the assistance of plant explorers of the United States Department of Agriculture, experiment-station officials, archaeologists, geographers, and botanists in various countries was solicited and abundantly received.

A study of the various forms of lima beans received indicated that the origin could be placed in the general region of Guatemala. A wild lima bean (plate 1, bean 1) recovered a number of times in this area satisfied deCandolle's concept concerning the wild original progenitor. The identification of this wild bean as a lima bean is justified by the fanlike radiations from the hilum indicated by Sturtevant (*39*) as the most reliable lima-bean character. Plants grown from this seed in the greenhouse made the identification conclusive. This wild lima bean possesses the smallest seed of the species found in any area. The increase in size

of the bean as it radiates from the Guatemalan center further emphasizes this point of origin. The dispersal of the lima bean is undoubtedly due to man. Under cultivation the size and other diversified characters were made to conform by selection to the desires of these primitive plant breeders. The concentration of diversified forms or varieties of lima beans has been found to be greatest in the Guatemalan areas by the Russian plant explorers (*8, 45*), a finding later confirmed by McBryde,[4] Standley (*37*), and other collectors. This conclusion concerning the point of origin satisfies the concept of Vavilov, which, taken with discovery of the wild progenitor, likewise agrees with the deCandolle concept and thus places the point of origin of the lima bean undoubtedly in the Guatemalan region.

The dispersal of the lima bean from the Guatemalan point of origin lies wholly in the hand of man under cultural conditions. Two important points related to the dispersal must be considered: first the genetic mechanism by which variations in form and habit may occur for use by the native plant breeders; and, secondly, the lines of dispersal over which the bean could travel. The first condition is answered by the almost general occurrence of hybridization due to insect pollination (*5, 28, 29, 30, 20*) and by rather infrequent mutations (*47, 33*).

LIMA BEANS IN PRE-COLUMBIAN TIMES

An indigenous bean which had undoubtedly never been under cultivation was found in the Guatemala jungles (plate 1, beans 2 or 45, or plate 2, bean 72). This bean may well correspond to the original bean from which all lima beans were derived.

The lines of dispersal from the point of origin have been defined by collections of wild lima beans, which are undoubtedly escapes from cultivation in pre-Columbian times (plates 1 and 2). The lines consist of three well-defined branches and one spur and are designated as follows: (1) the Hopi, or northern, branch, (2) the Carib, or West Indies, branch, including a spur terminating in Socorro Island about 400 miles off the west coast of Mexico, and (3) the Inca, or southern, branch.

The three lines follow the trade routes rather than travel routes. The Indian tribes along these routes are known to have traded shells and other things, and it is well known that seeds of all kinds were eagerly sought. This desire for new crops persists strongly even today and accounts for the appearance of post-Columbian plants like the watermelon, which apparently arrived in the southwestern United States ahead of European explorers (*10*).

[4] Collections made by Dr. F. W. McBryde, Fellow in the National Research Council.

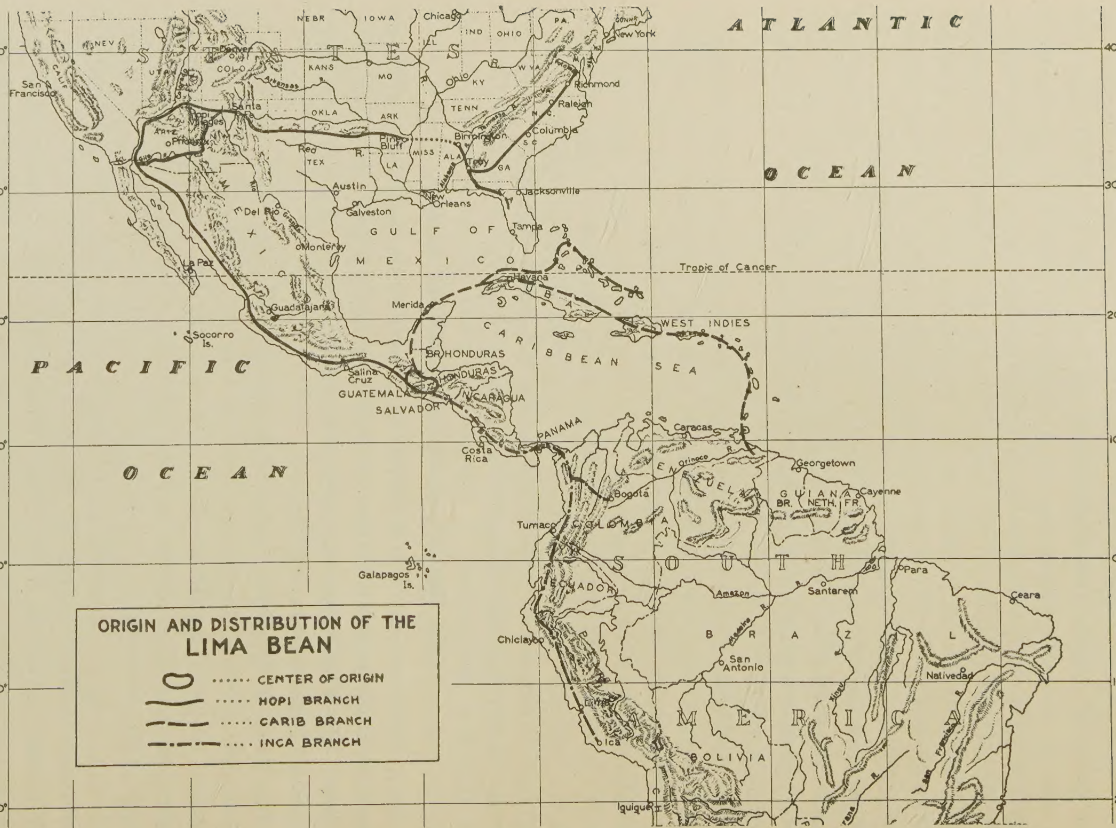

Fig. 1. Lines of dispersal of the lima bean, *Phaseolus lunatus*, from the point of origin in Guatemala.

The Hopi, or Northern, Branch.—Representative beans of the Hopi branch are shown in plate 1, beans 1 to 43. This branch (fig. 1) proceeded from the Guatemalan point of origin along the western slopes of the Sierra Madre in the zone above the *tierra caliente* as indicated by existing specimens of lima beans recovered from cultivated fields. These beans may have entered the United States by way of Yuma, Arizona, where they have been found, or further to the east by way of the Papago and Pima Indian tribes. The lima beans in the fields of the Papago and Pima tribes and those found in the Hopi pueblos are closely related. That the passage may have been up the Colorado River through the Colorado River tribes and the Walapai (or Hualpai) and Havasupai tribes is indicated by the even closer relationship between the beans grown by the latter and by the Hopi; some doubt exists, however, because of geographical barriers. That these beans have existed in these areas since pre-Columbian times is attested by the lima beans found in pre-Columbian ruins (*38*). The northward extension was terminated by unfavorable temperatures and high altitudes, for no lima beans have been found in the cliff-dweller ruins at Mesa Verde, although prehistoric specimens of *Phaseolus vulgaris* and *P. coccineus* have been found.

A trade route undoubtedly existed between the Guatemala area northward to the Indian tribes of the Southwest. Corroborative evidence was shown by Sauer,[5] who found in prehistoric ruins the skeleton of a Guacamayo macaw indigenous to southern Mexico and southward. Whiting (*48*) and others record the finding of Jack beans (*Canavalia ensiformis*) in pre-Columbian ruins.

Wild and cultivated species of *Canavalia* are found today growing in Guatemala. The seed of these tropical species planted in California at Davis did not mature seed owing to photoperiodism, that is the effect of length of day (*16*), whereas plants derived from seed grown in northern latitudes matured perfectly. This condition indicates that many years or generations may have been consumed in transporting these beans northward to the Arizona sites.

The tepary bean (*Phaseolus acutifolius*) is indigenous to Arizona, where it has no doubt been developed to its present size and productivity by Arizona agricultural tribes. The tepary bean was found under cultivation in Guatemala by McBryde; it differed in no way from certain varieties found today in Arizona. It showed, however, no wide diversity of form and color in the seed, a fact which indicates the southward transportation of the tepary bean along a trade route. On the other hand, the

[5] Collections made by Dr. Carl O. Sauer, Professor of Geography, University of California, Berkeley.

characteristics of the lima beans in the Arizona region are all found in the lima beans of the Guatemala area, but many forms in Guatemala do not occur in Arizona or in the eastward extension of lima-bean culture (plate 1).

The lima beans found by early explorers from Florida to Virginia (*10*) along the eastern slopes of the Appalachian Mountains differ in no way from those found in the Hopi pueblos at the present time. The lima beans cultivated by the Cherokee Indians of Georgia and other Indian tribes of the Atlantic Coast closely resemble those grown by the Hopi Indians. The route for the dispersal of the lima bean eastward across the Mississippi Valley is obscure and somewhat indefinite. Evidences of bean culture, however, are found as charred remnants in caves (*17*) as far east as Pine Bluff in Arkansas. A possible route could have passed from the region of Albuquerque, New Mexico, along the Red River skirting the Ozark Mountains. At Rocky Ford, Colorado, Hopi lima beans have become a well-established crop. In the Texas Panhandle and in Oklahoma the Hopi bean has been found well adapted. Other cultures of lima beans were found eastward to the Mississippi River. There still remains a gap across the Mississippi Valley to the western slopes of the Appalachian Mountains (fig. 1). From the southern Appalachians in Alabama into Florida and northward to Virginia, cultivated lima beans identical with those cultivated in the Hopi pueblos are found. In the Gulf states of Mississippi, Alabama, and Florida, Small (*35*) found similar lima beans; these are still found in a wild state in thickets, undoubtedly escapes from pre-Columbian cultivation (plate 1).

The Henderson Bush (plate 1, bean 39), the first small, or baby, lima to be extensively cultivated in California and elsewhere, started from a chance plant selection in Virginia, originally coming from Indian cultures (*18*). This variety or others identical in every way with it have been recovered frequently from hybrid Hopi limas.

Over the Hopi trade route may have been carried eastward seeds of common beans (*Phaseolus vulgaris*), corn, and squashes. Along portions of this route, in ancient ruins and middens, have been found shells, flints, beads, and seeds from the Pacific Coast area. The northern California black walnut (*Juglans Hindsii*), extensively used as rootstock for California walnut orchards for the existing groves (*36*), is found only immediately adjacent to Indian *rancherias* in the Sacramento Delta and in the San Francisco Bay region. This walnut so closely resembles the common black walnut of the Mississippi Valley as to confuse botanists (*23*) and may well have been carried westward over a trade route.

Gilmore (*17, 42*) presented a possible route for corn arriving from

Mexico at Del Rio, Texas, and following along the Edwards escarpment to the Red River and thence eastward. He was not entirely satisfied with the route, and it appears more probable that the Hopi trade route was used not only for lima and common beans but for corn and squashes.

The Carib, or West Indies, Branch.—From its initial start in Guatemala, the Carib branch passed along the western slopes of the mountains to the lowlands of the Isthmus to Tehuantepec (*8, 37*), across to the coast of the Gulf of Mexico, and thence easterly along the dry calcareous lands of Yucatan, where Standley (*37*) and Bukasov (*8*) found lima beans in both the wild and cultivated state. Apparently this route is the only one eastward, except the Hopi route, which possesses climatic conditions suitable to the lima bean. The eastern slopes of the Sierra Madre are nowhere favorable to lima beans in the wild state. The reason appears to lie in the excessive rainfall or humidity throughout the year, for the lima bean requires a somewhat arid climate for a portion of the year. The arid condition of the Yucatan peninsula favors the culture of lima beans. From the easterly tip of Yucatan the lima beans were undoubtedly transported in the canoes of the Carib Indians to Cuba and thence to all the islands of the West Indies where they have been found. This route lay by way of the Greater and Lesser Antilles to the northern coast of South America. From this point the lima bean has probably been extended to all parts of Brazil where it has been found by various botanists (*14, 6, 27*). Evidently, however, the rainy basins of the Orinoco and Amazon rivers were unfavorable to it, for no wild limas are found in these regions. Pittier (*32*), who has made extensive studies of beans in Costa Rica and elsewhere in Central America, reports that no wild limas were found in Venezuela proper, and only on two small islands off the northeast coast have wild beans been recovered.[6]

In tracing the Hopi and Carib branches (fig. 1), it will be noted that the distance between Cuba and Florida is very short; yet the lima beans of Florida and Cuba are definitely of distinct groups. The moist lowlands of southern Florida are unfavorable to lima beans. This condition could have been overcome if water travel had carried the Carib type of lima bean to northern Florida. This gap, however, was not bridged, as evidenced by the distinct differences between the groups of lima beans.

The Hopi branch is usually rather flat and medium in size, whereas the Carib branch, as was found by Bukasov (*8*) in Yucatan, includes many oval or roundish beans of the potato type, frequently of bright-red color, characters absent in the Hopi limas. Typical shapes and colors of the Carib branch are shown in plate 1, beans 44 to 53, and plate 2, beans

[6] H. Pittier, letter to W. W. Mackie, dated April 20, 1939, at Carácas.

54 to 70. The greatest and most distinctive difference lies in the cyanide content. All lima beans contain cyanide, due to the glucoside, linamarin. Lethal doses of this poison in Puerto Rico and elsewhere have been reported. This condition led to an extensive survey of the cyanide content of lima beans from all areas for the three branches, but only in certain varieties of the Carib branch was the content sufficiently high to be dangerous as human food. The high cyanide content appears to be inherited, for not all varieties of the Carib branch contained dangerous quantities. The linamarin of lima beans will be discussed further under "Cyanide Content."

Wild lima beans collected on Socorro Island of the Revillagigedo group in the Pacific Ocean by Mason (*24*), on a botanical expedition, appear to be a spur of the Carib branch; for they differ from the Hopi branch, to which they are closer geographically, in the flatness of the seed and the high cyanide content. Evidence of the latter is the poisoning of the crew of Captain Colnett's (*12*) expedition in 1798 by eating wild lima beans found growing on the island. The beans seem to have arrived here at an early date. That they were brought to the island by Indians in canoes is very probable, for the author can vouch for the seaworthiness of the Indian canoes from personal experience. The beans (plate 1, bean 46) are only slightly larger than the wild progenitors in the jungles of Guatemala. They are perennial and truly tropical in habit. Seed collected by Mason would not fruit under California conditions, owing to photoperiodism.

The Inca, or Southern, Branch.—Like all other lima beans, the Inca branch originated in the Guatemala region. This branch (representative beans are shown in plate 2, beans 71 to 96) is best distinguished by the extreme sizes reached in pods and seeds—the largest bean (plate 2, bean 93) being over 31 times the weight of that of the small, wild progenitor of all lima beans (plate 1, bean 1). An increase in size of seed or fruit is usual in the processes of breeding by selection. The passage of maize southward from the Aztec to the Inca civilizations shows a great increase in the size of seed and plants, culminating in the large-seeded Cuzco floury maize of Peru.

McBryde found a wild lima bean of large size but flat, thin, colored, and mottled (plate 2, bean 78); this may well have been the type from which the large lima bean descended.

In the passage southward through Central America, Colombia, Equador, to its final termination in Peru, many forms, sizes, and colors were retained. These forms find their widest range and highest altitude in Colombia in the region of Bogotá. As the culture of the lima bean passed

southward into the more arid and unfavorable regions of Peru, the plant breeding for adaptation was intensified. The culmination of these breeding efforts was reached in the region of Ica on the coast south of Lima, Peru. Here the long, cool, dry summers resulting from the upwelling of the Peruvian, or Humboldt, Current forced the very restricted adaptation found in the modern large lima beans, all of which originate from this source.

Many colors, including red, black, brown, and mottlings thereof, have been recovered from ancient Peruvian tombs (*49*). The preference for white over color in these large lima beans appears to be related to the ease by which this color is fixed, for it is recessive to all other colors. Various colors and mottlings are still found in the Inca group.

The fact that continued increase in size can be achieved by breeding indicates that a number of factors, or genes, are involved; polyploidy is not involved, for the chromosome number has never been found to change (*25*). The potato, or oval, shape of seed probably appeared among the progeny of field hybrids and was selected by ancient plant breeders. The effect of early breeding upon modern varieties will be discussed under dispersal in the following section.

LIMA BEANS IN POST-COLUMBIAN TIMES

Since the discovery of America, lima beans have been widely distributed, especially in the tropics, where they find conditions closely resembling those where they originated. Each of the three branches—Hopi, Carib, and Inca—has contributed to modern horticultural varieties. It is possible to determine with a fair degree of accuracy from which branch a modern horticultural variety has been derived.

The Hopi branch was first encountered in post-Columbian times along the Atlantic Coast. From the Indian tribes found cultivating lima beans, such varieties as Jackson's Wonder, Sieva, Small White, Carolina, Carolina Sewee, Willow-leaved, Henderson Bush, Woods' Improved, and many others have been derived. Lima beans grown by the Hopi and southwestern Indians were the basis for several varieties bred by the author. These varieties include Hopi 2000, Hopi 155, Hopi 56, Hopi 5989, and Hopi 12. All of these possess various degrees of resistance to the attacks of the root-knot nematode and have been of outstanding value in areas badly infested with this pest.

The color patterns of the seed coats of the varieties found among the Hopi pueblos so closely resemble those of similar varieties derived from the Indians of the Atlantic Coast that sharp distinctions are not possible. The author has selected, from Hopi strains heterozygous in the field,

such types as Jackson's Wonder, Henderson Bush, Willow-leaved, and many others. At the same time, such types as the sulfur-backed, green-eyed Hopi 2000, Brown Hopi, Red Hopi, and Red Mottled Hopi—all of the medium-sized seed type—have not been recovered from the Atlantic seaboard (plate 1). It appears from these and other observations that this and other types found in the Hopi agriculture did not pass on to the Atlantic Coast. This condition agrees with Vavilov's concept which provides for a reduction in the number of forms as the culture is extended from the common center of origin.

The Carib branch in post-Columbian times has been widely dispersed. It is distinguished not only by the bright-red-colored types but principally by the occurrence of types or varieties bearing cyanide in lethal amounts. Inasmuch as the first explorers in America encountered the Carib branch, it has become widely distributed, especially in tropical areas over the whole world. The Manila galleons in their passage across the Pacific from the Philippine Islands to Mexico transported lima beans of the Carib branch from the West Indies. These limas escaped from cultivation and became established in the Philippine Islands and in near-by regions. Probably from this source also came varieties of the group found at present in Java, Burma (*41*), Mauritius (*47*), and other East Indies areas. Many varieties of lima beans found in the East Indies have been reported as bearing excessive quantities of cyanide (*11*). In Africa also (*43*) varieties of the Carib branch have been recovered, but the direct connection with the West Indies has not been recorded. It is likely that these lima beans were carried to various parts of Africa from Brazil through the slave-trade operations as was the peanut, which reached interior African tribes ahead of the first European explorers. Further explorations will doubtless extend the range of this group in tropical areas.

The Inca branch in the post-Columbian period has given to horticulture the largest number of varieties and has received the most widespread and extensive distribution of all the lima beans. All the modern varieties of large lima beans trace back to Peru, and these in turn to a Guatemalan origin. The discovery of large lima beans of various types in the ancient tombs of Peru (*49*) points to the vast age of this branch and indicates the fixity of many characters such as color, size, shape, and adaptation to the peculiar climate of the Peruvian coast, where the modern large lima bean was developed subject to the influence of the Peruvian Current. The persistence of these characters has restricted the commercial production of dry limas (the Inca, or large-lima, type) to areas with climates somewhat similar to that of the Peruvian coast.

Many varieties (*18, 19, 43*) have been introduced into Europe and into the eastern United States from Peru, but beyond affording varieties restricted to gardens, they have not become established as a major crop. In Madagascar, Peruvian large limas were introduced at an early but unrecorded date. The identification of the Madagascar large lima with the Peruvian bean is complete, for the whole list of characters found in the Peruvian types are also found in the Madagascar large-lima varieties. On this large island in the southern part of the Indian Ocean conditions exist which satisfy the requirements of this exacting bean. According to Rimbaud (*33*) the long growing season common to the Peruvian types was found undesirable in certain Madagascar districts because of water shortage. Taking advantage of variability due to heterozygosity common to lima beans, the Madagascar farmers on the southwestern arid coastal areas established early-maturing varieties by plant selection. In some of these varieties early maturity was linked with smaller size of seed and smaller vines. It was probably one of these varieties that was the foundation of the large-lima-bean industry in southern California. The first of these introductions was made, according to accepted reports, by the captain of an American clipper in the Mexican era before American occupation of California. Forms of these early-maturing Madagascar large lima beans were recently tested in Ventura County and found to resemble closely the Lewis variety (*19*) from which the majority of field varieties grown in California originated.

In Burma (*41*) lima beans have been grown extensively, but in these beans cyanide frequently appears in dangerous amounts. This indicates that they may have been derived from the Carib branch; but their present large size perhaps points to a cross in the field with beans from the Inca branch (*29, 20*).

The greater number of the large-lima-bean varieties offered by seedsmen in the United States have arisen from plant selections made in California. The practice of contracting with California lima-bean farmers for seed of varieties of large lima beans grown in gardens in the eastern states furthered the creation of new varieties by plant selection. This process is made possible by field crossing due to insects (*28, 30*); crossing may occur not only within a group such as sievas but also between the sieva and large-lima group.

CLIMATIC ADAPTATIONS

The lima bean, as indicated by its behavior in its place of origin in Central America, is a perennial viny plant, usually with an enlarged rootstock for the storage of starch. Annual and small bush forms, how-

ever, have appeared after hybridization. Only in tropical or subtropical areas does it escape from cultivation and maintain itself in a wild state. Low-lying coastal areas of the *tierra caliente* are not usually acceptable to the lima bean, which prefers sloping or well-drained areas above the *tierra caliente* to an altitude of 6,000 feet in the tropics and of 3,000 to 4,000 feet in some of the temperate zones. Climates best suited provide a dry season for the maturing of the seed. Ability to withstand severe drought until the next rainy season is characteristic. In the hands of the Hopi and other southwestern tribes, the lima bean produces crops without irrigation, the crops depending entirely upon the scanty rainfall of these arid regions. Cultivation is scanty and consists almost exclusively of planting, of weed eradition, and of protection against wind. Hopi limas surviving these severe conditions have provided hardy stocks useful in breeding against drought and diseases.

The sieva, or small-lima, group includes varieties much more resistant to heat and arid conditions than the large-lima group. On this account many of these varieties can thrive in the more continental climates of the interior. For this reason the sieva varieties are spread over a wide range in North America, Central America, South America, and the West Indies. On the other hand, the large-lima group is restricted to the coastal areas, where extremes of heat do not occur and where the air is more highly charged with moisture, usually in the form of fogs, in the growing season. Both groups are fairly drought-resistant, and for this reason the perennial types survive and thrive where rainfall is deficient over a considerable portion of the year. The perennial habit, which is the usual form for the wild limas, is found in both large- and small-lima groups. In resistance to cold there appears to be little difference.

The lima bean usually requires a long growing season free from frost, varying from about 100 days for the earliest varieties grown in the United States to seven to nine months for the large-lima varieties of Madagascar and Peru. At maturity the pods of many of the wild types shatter badly in rainy seasons; but selective breeding has provided non-shattering varieties under cultivation.

Photoperiodism, or the effect of length of day upon plants, is pronounced in lima-bean varieties long established in the tropics. Such varieties when planted in temperate zones do not fruit until the lengths of day and night are about equal. Garner and Allard (*16*) noted this effect in beans from Peru and Bolivia. This condition prevents the production of seed in the temperate zones because of the appearance of cold weather and frost before normal maturity has arrived. All wild lima beans from the tropics show this behavior; they completely fail to

fruit. Some of the cultivated varieties, however, ripen seed; from this seed, plants were secured that possessed disease and pest resistance. Lima-bean seed originating in the temperate zones did not fail to set seed in the normal manner. How much time is required to correct the effect of photoperiodism in the passage of the beans northward from Guatemala cannot now be calculated, but undoubtedly a long time was required. The separation of the Carib and Hopi branches by photoperiodism is sharply marked, for this response is usually found in all the Carib beans grown in the tropics and never in the Hopi beans from the north temperate zone.

CYANIDE CONTENT

The specific unity of lima beans is indicated by a common physiological character, the occurrence of cyanide containing the glucoside, linamarin (*2*). The glucoside is common to all lima beans and imparts the characteristic flavor that is absent from other species of beans.

Cyanide, however, is found in many fruits and in forage plants, including the almond, peach, apricot, and sorghums. The flavor which the linamarin imparts is, when the amount is not in excess, desirable and in no way injurious. The Pure Food Law of the United States places the limit for the injurious quantities to humans at 100 p.p.m. of HCN. In Puerto Rico, McClellan reports that 300 p.p.m. of HCN was lethal when fed to chickens and killed most of them. Reports from this area and others of lethal effects on humans have been recorded. One lot of wild lima beans from Puerto Rico analyzed 970 p.p.m. cyanide as HCN and gave off the characteristic bitter-almond odor when briskly rubbed (plate 1, bean 47). In Burma (*11, 46*) considerable trouble was occasioned by excessive quantities of cyanide, which frequently prevented export. In India the same trouble arose from lima beans of the roundish small type—both red and white—in seed from Mauritius that evidently derived from the Carib branch.

A careful survey of lima beans of all classes grown in California demonstrated conclusively that no varieties derived from either the large (Inca branch) or the small (Hopi branch) limas contained dangerous quantities of cyanide, the quantity ranging from 25 to 55 p.p.m. as HCN, which is far below the limit of tolerance set by law (100 p.p.m.). In order to determine the effect of tropical environment upon cyanide content of lima beans, standard varieties of large and small limas of the United States were grown in experiment stations in the coastal regions of Georgia and at Mayaguez, Puerto Rico. The seed from the resulting crops in both areas contained, on analysis, slightly lower quantities of

cyanide than the original seed from California. Large lima beans from Madagascar showed no objectionable quantities of cyanide (25 to 75 p.p.m. as HCN). The Madagascar beans are unquestionably from the Inca group and have been grown in the tropics for a long time. It becomes apparent from the evidence that different degrees of cyanide content may be inherited as genetic characters. Control of cyanide content may therefore be effected by breeding methods.

DISEASES AND PESTS CHARACTERISTIC OF LIMA BEANS

Disease and insect pests are frequently specific and to this extent may be used to distinguish host species. The genus *Phaseolus* is divided into two groups of species—Asiatic and American. The most important group includes those originating in the Americas, such as *Phaseolus vulgaris* (kidney bean), *P. lunatus* (lima bean), *P. coccineus* (multiflorus, or butter, bean), and *P. acutifolius* (tepary bean). The Asiatic group indigenous to that continent includes *P. Mungo* (urd bean), *P. aureus* (mung bean), *P. angularis* (adzuki bean), *P. calcaratus* (rice bean), and *P. aconitifolius* (moth, or mat, bean). These Asiatic species are all susceptible to the fungus disease caused by *Cercospora cruenta* (*21*) but not to *Gleosporium lindesmuthianum,* whereas the American species are resistant.

While many general fungus diseases, like *Fusarium martii, Rhizoctonia solani,* and *R. bataticola,* and pests, including wireworms, root-knot nematodes (p. 15), red spider, and thrips attack the lima bean, many diseases and pests are more specific. The lima bean downy mildew caused by *Phytophthora phaseoli* (*40*), scab caused by *Elsinoe phaseoli* (*7, 22*), and pod blight caused by *Diaporthe phaseolorum* appear to be specific for all lima beans. The lima bean pod borer, *Etiella zinckenella* (*13, 4*), harbored by native lupines, confines its attacks principally to all types of lima beans. The specificity of these diseases and pests further tends to establish the unity of all lima beans as one species.

INHERITANCE OF SOME IMPORTANT GENETIC CHARACTERS

In breeding for disease resistance and improvement in yield and quality, hundreds of crosses were made with the usual fertility found in hybrids made within the same species. The chromosome numbers for all lima beans is the same—namely, haploid 11 and diploid 22 (*25, 34*). The following genetic ratios were found in lima beans whether the

crosses were made between varieties of a single group or between varieties of opposite large- and small-lima groups usually classified as distinct species.

Vine dominant over bush	ratio 3 : 1
Color dominant over white	ratio 3 : 1
Flat, thin seed dominant over potato type	ratio 3 : 1
Mottling dominant over self-color	ratio 3 : 1
Colored inflorescence dominant over white	ratio 3 : 1
Broad leaf dominant over willow leaf	ratio 15 : 1
Size intermediate in F_1	multiple factors
Resistance to root-knot nematodes dominant	multiple factors

Anthocyanin color in leaves and stems is lethal to the plant in the homozygous condition.

Although this list is limited, it shows no inherited difference that would warrant species distinction. Further genetic studies now being carried on seem unlikely to disturb this conclusion.

In all the groups of lima beans, strains or varieties have been found resistant to the root-knot nematode. The first discovery, made by the author in 1923, arose when breeding lima beans from the Hopi Indians in northern Arizona (*15*). A number of varieties were recovered, like Hopi 2000, but others like Hopi 155 (plate 1, bean 42), Hopi 5989 (plate 1, bean 41), and recent crossings with the common Wilbur (plate 1, bean 40), were created by hybridization.

In an endeavor to place nematode resistance in large lima beans, crosses were made with nematode-resistant Hopi varieties. In backcrossing these hybrids to the large lima, it was found that size was increased only slowly and with difficulty, owing to the multiple factors involved. From an importation from Peru of a mixed lot of large lima beans, a plant was discovered which bore very large seeds and possessed superior resistance to nematodes. This strain, in addition, developed considerable resistance to wireworms. Even though five years of breeding for nematode resistance in large limas was involved, it was found desirable to start breeding afresh, using the new nematode-resistant Peruvian large lima.

Tests with small limas yielded a number of nematode-resistant forms, one of which showed the highest resistance yet discovered. The multiple factors which combine to produce nematode resistance in lima beans appear to be the same in all lima beans and provide convincing evidence of the unity of the species.

NOMENCLATURAL HISTORY AND PRESENT TAXONOMIC STATUS

The lima beans encountered by the early explorers included many forms and colors in seeds and various forms of vines. These were frequently interpreted as multinomial species by the pre-Linnaean botanists. The drawing of a bean vine and seed in Lobel's *Icones* (*18*) is undoubtedly that of a small-podded, or sieva, lima, bearing the name *Phaseoli parvi pallidoalbi ex America delati*. Clusius, 1601, noted many forms of vine and colors of seed. Bauhin, 1651, and others listed several forms. Linnaeus, 1753 (*26*), in his book *Species Plantarum* listed two species—*Phaseolus lunatus,* a small, or sieva, lima and *P. inamoenus,* a large lima.

A post-Linnaean chronological list of lima-bean species compiled by Van Eseltine (*43*) includes the following:

Linnaeus, 1753
- *Phaseolus lunatus*—small white sieva
- *P. inamoenus*—speckled large lima

Jacquin, 1770
- *P. rufus*—red sieva, or Mauritius bean
- *P. bipunctatus*—spotted sieva

Medicus, 1787
- *P. achariensis*—sieva

Louriero, 1790
- *P. tunkinensis*—red-mottled sieva

Moench, 1794
- *P. macrocarpus*—large, speckled

Zuccarini, 1809
- *P. Xuarezii*—dwarf or bush sieva

Stokes, 1812
- *P. saccharatus*—sieva
- *P. parviflorus*—sieva

Poiret, 1813
- *P. macrocarpus*—large white

Schrank, 1819
- *P. derasus*—black-seeded Brazilian sieva

Kunth, 1823
- *P. puberulus*—yellow sieva

Roxburgh, 1832
- *P. maximus*—large white

Blanco, 1837
- *P. ilocanus*—red-mottled sieva
- *P. vexillatus*—large white

Macfayden, 1837
- *P. dumosus*—large white
- *P. limensis*—large, white, plump seed
- *P. foecundus*—large, oval, white
- *P. saccharatus*—white or red sieva
- *P. latisiliquus*—large white

Bentham, 1859
- *P. lunatus*—small-podded sieva
- *P. bipunctatus*—as synonym
- *P. lunatus* var. *macrocarpus*—large-podded

Bailey, 1924
- *P. lunatus*—small-podded sieva
- *P. limensis*—large-podded

Piper, 1926
- *P. lunatus* L.—all lima beans

Van Eseltine, 1931—five formae

P. lunatus forma *macrocarpus*	Van Esel. flat lima
P. lunatus forma *salicis*	Van Esel. willow leaf
P. lunatus forma *lunonanus*	Van Esel. bush sieva
P. lunatus forma *limenanus*	Van Esel. bush lima
P. lunatus forma *solanoides*	Van Esel. potato lima

Beginning with those described by Linnaeus, the 26 variously listed "species" may be included in two groups: the large-podded and the small-podded types. Species distinctions made by the various botanists were based on characters that do not warrant species rank, as was shown in the preceding section. The basic distinctions included vine variations (bush, vine, and intermediate), annual and perennial habit, leaflet form (willow leaf, large and small size), size and shape of pod, pod points, number of seeds per pod, warty serrations on pod sutures, seed-coat-color distributions, radiations from the hilum, shape of seed, including flat, oval, and others. Bailey (*3, 4*), following the example set by Linnaeus (*26*), recognized two forms—the large-podded type, which he listed as *Phaseolus limensis,* and the small-podded types, which he included under *P. lunatus.* Piper (*31*), who devoted years of research to the study of American Phaseolinae, states: "This is a very diverse aggregation of both wild and cultivated forms, whose status is variously interpreted by different botanists. In the writer's judgment, it is but a single botanical species." Van Eseltine (*43*), who concurs in Piper's concept of a single species for lima beans, employs five "formae" to include the many genic variations. The formae are outlined as follows:

Phaseolus lunatus L. The small lima, or sieva, bean. The leaves of the typical forma are relatively thin and small, as are the pods.

a) Forma *macrocarpus* Van Esel. Flat lima. Pods and leaves are thicker and larger than are those of the typical form.

b) Forma *salicis* Van Esel. Willow leaf. This forma has narrow lanceolate leaflets, but otherwise resembles true *lunatus*.

c) Forma *lunonanus* Van Esel. Bush sieva. This dwarf forma arises from the production of inflorescences from both the terminal and distal axillary buds after the plant has developed from 4 to 8 nodes. This forma also includes a type in which the first 3 or 4 nodes produce long axillary branches.

d) Forma *limenanus* Van Esel. Bush lima. Dwarf limas are counterparts of the preceding form, except for pod and leaf characters.

e) Forma *solanoides* Van Esel. Potato lima. This forma has leaflets somewhat narrower and more triangular than those of the flat limas, the pods are slightly shorter, and the seeds are more nearly circular in cross section. Otherwise the plant resembles the true lima.

These five formae, which appear to be six if the sieva, or small-podded, lima is included, offer no more marked or serviceable distinction for botanical rank than do the usual horticultural varieties. For example, formae *a* and *b* are both large limas, separated on the shape of the seed, the former being flat and the latter more nearly globular. These characters have been exchanged from vine to bush by artificial hybridization, at which times all intermediate shapes were isolated. The same situation holds true in regard to forma *b* and other types of leaflets. This willow-leaf forma has been transferred to many types or varieties of lima beans in the large and small groups. Likewise formae *c* and *d* are separated as sieva bush and large-lima bush, respectively. The bush character, which appears the same in both large and small limas, has been transferred by breeding methods at will into any form of lima bean as a single character, or gene. None of the five formae are separated on a basis which cannot be restricted to a comparatively few genes.

Bailey (*3, 4*), in support of his separation of lima beans into two species, used certain distinctions which Van Eseltine (*43*) has tabulated:

	Large lima (*Phaseolus limensis*)	Sieva, or small, lima (*Phaseolus lunatus*)
Duration	Perennial	Annual
Calyx	Linear	Ovate
Bracts	One third length of calyx; not strongly veined	Nearly, or quite, equaling calyx; strongly veined
Pod	Thick-edged; blunt, short tip	Thin-edged; sharp, long beak
Leaves	3 to 5 inches long; thick	2 to 3½ inches long; thin
Seeds	White	Various colors
	Plump	Flat and thin
	Larger	½ inch long

While Bailey has endeavored to place all lima beans under two species conforming to the commercial groups of large and small, or baby, limas, this species distinction is not borne out by the character differences in the forms now available. For example, perennial and annual forms have

been found in both large- and small-podded types, although perennial forms appear more common. In certain protected areas of California, perennial types of limas have persisted.

The linear and ovate forms of calyx bracts and bract veins are not sufficiently defined for species distinction. Bailey found the broad calyx form included 76 per cent of the sievas and 66 per cent of the large limas.

Pod distinctions, however, appear more strongly marked, and the groups with large and small pods are further set apart by the length and sharpness of the pod points.

Leaf characters which Bailey uses are not sufficiently distinct for use in this separation. The size of the leaf in many cultivated large limas is greater than that of the commonly cultivated small-podded lima. On the other hand, collections of lima beans from a wide range of sources present a contrary set of evidence, for many small-podded limas possess the largest sizes of leaves. Willow-leaf types as well as intermediate grades are found in both classes. Very dark-green colors, commonest in the small-podded types, are also found in the large-podded types.

Seed color as a basis for species separation is completely unjustified (plates 1 and 2), since all possible colors, shades, and mottlings are found in both groups. The shape of the seed likewise fails. All shapes occur in both groups. For example, the potato type (Van Eseltine's forma *solanoides*) occurs naturally in both large and small limas, and can be transferred at will by artificial crossing. Size, however, is more reliable for group separation, since seeds of the large-lima varieties are distinctly larger and usually possess more distinct radiations from the hilum. The pitting, or dimpling, of the large lima is usually, but not always, absent in the sieva, or small, lima. The number of seeds per pod in the sieva varieties is usually 3, but many pods contain only 2 beans—rarely 1 and 4. In the large lima the usual number is 4 for the commercial varieties, but 5 and even 6 may be found, and 3 seeds are frequent and common; 2 and 1 are rare and are due usually to poor growing conditions for the plant.

SUMMARY AND CONCLUSION

Numerous species and varieties of lima beans recognized by botanists may be included in a single species, *Phaseolus lunatus* L. The many forms of vines, pods, and seeds found in lima beans are the result of genic, or character, differences brought about by field hybridization (due to insects) or by mutations common to this species.

Genetic evidence and cytological evidence unite to point to a single species of lima beans because artificial crosses have proved fully fertile and in all so-called "species" and forms the haploid number is 11 and the

diploid 22. The genetic inheritance of the various characters of lima beans is unchanged no matter which of the so-called "species" or formae are involved in the crosses.

While many diseases and pests found attacking lima beans attack other hosts, a number of fungus diseases and insect pests are specific in their attacks on lima beans. This is further evidence of the unity of all lima beans as one species.

Geographical distribution from the original source of the wild progenitor in the Guatemala region indicates three lines, namely: (1) the Hopi branch, extending northward in areas in the United States, (2) the Carib branch, carried to islands in the West Indies and to the Amazon basin, and (3) the Inca branch, which traveled south from the Central American point of origin to Peru. These lines of dispersal followed the trade routes of the Indians in pre-Columbian times and are identified by the characteristics of the varieties of beans included in them. Progressive improvement in size and form of the wild lima and in the quality of the bean followed the departure from the source of origin.

The dispersal of lima beans in the post-Columbian period is determined by the character of the beans identified in the established three pre-Columbian groups.

A knowledge of the origin and dispersal of the lima bean, the unity of the species, and the specificity of its diseases and pests, may be used by the plant breeder in creating useful horticultural varieties.

The concept of deCandolle of the origin of cultivated crops (recovery of a wild progenitor) and the concept of Vavilov (concentration of species and forms) agree in placing the origin of the lima bean in the Guatemala region.

The unity of all lima beans in a single species is supported by the presence of the glucoside, linamarin, the result of two enzymes imparting the characteristic lima-bean flavor found in no other bean.

The evidence presented supports Piper's contention that all lima beans belong to a single species, *Phaseolus lunatus* L.

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PLATES

DESCRIPTION OF PLATE 1

Bean no. and description of seed	Grams per 100 seeds	Place collected
HOPI BRANCH:		
1. Indigenous, lenticular, brown mottled	6.94	Guatemala
2. Indigenous, lenticular, hilum radiations	9.5	
3. Brown mottled, flat	17.5	Socorro Island, Mexico
4. Red, flecked	76.0	Hopi Reservation, Arizona
5. Black, pitted	60.0	
6. Bush, black	75.0	
7. Bush, white	74.0	
8. Bush, white	83.0	
9. Bush, red	111.0	
10. Red	54.3	
11. Dark red	71.4	
12. White, dull, split seed coat	58.6	
13. Purple star dust or white	49.2	
14. Star dust + dark-red dorsal	61.5	
15. White, bright	49.0	
16. White, dull	53.0	
17. Dark red + light-red blotches	88.0	
18. White, plump, sulfur dorsal	64.0	
19. White + pale greenish	52.4	
20. Light red + dark-red spots	62.0	
21. Dark red + black spots	81.4	
22. Black + brown flecks	74.0	
23. White + star dust, black dorsal	92.8	
24. White + star dust, dark-red dorsal	56.8	
25. Dark red + black blotches	44.0	
26. White + star dust + dark- and light-red striations	85.2	
27. White + star dust + dark red	46.6	
28. White + star dust + dark-red dorsal	55.7	
29. Dark red + light-red blotches	40.5	
30. Black	46.5	
31. Willow-leaf sieva, white	47.4	Colorado
32. Bush sieva, white	71.5	Carolina
33. Jackson's Wonder, brown and dark-red blotches, Atlantic seacoast	47.8	
34. Jackson's Wonder, brown and red flecks	44.3	Atlantic seacoast
35. Florida red + speckled	77.2	
36. Hopi brown + black striations	61.1	Hopi Reservation, Arizona
37. Hopi white + star dust + red, dorsal	44.4	
38. Hopi dark red + black flecks	66.3	
39. Henderson Bush, white	53.8	California (commercial varieties)
40. Wilbur, vine, white	44.0	
41. Hopi 5989, white, nematode-resistant	56.2	
42. Hopi 155, white, nematode-resistant	53.6	
43. Hopi 56, white, dry-rot resistant	47.0	
CARIB BRANCH:		
44. Indigenous, lenticular, brown mottled; same as bean no. 1	6.94	Guatemala
45. Indigenous, black	13.8	
46. Brown mottled, flat; same as bean 3	17.5	Socorro Island, Mexico
47. Cyanide as HCN, 970 p.p.m.	45.4	Puerto Rico
48. White + dimple	44.0	
49. White + sulfur dorsal	51.2	
50. Dark red	65.9	
51. Bright red + black globular	31.7	
52. Bright red + black flecks	42.2	
53. Dark red + black fleck, globular	42.4	

DESCRIPTION OF PLATE 2

Bean no. and description of seed	Grams per 100 seeds	Place collected
CARIB BRANCH (*concluded*)		
54. Flat red + black spots	46.2	Puerto Rico
55. Dark red, globular	41.1	
56. Pure brown	45.3	
57. Brown + black flecks, globular	44.1	
58. Brown + black flecks, globular	30.3	
59. White, oval	44.5	
60. White star dust + dark-red dorsal, oval	54.5	
61. White star dust + red striations, oval	49.8	
62. Dark red + light-red flecks, globular	34.1	
63. Flat, brown + dark-red striations	54.8	
64. Flat, dull red + flecks	58.4	
65. Dark red + dimple	59.9	
66. White, plump, dimple, sulfur dorsal	61.0	Cuba
67. White star dust + dark red	54.8	
68. White, yellowish, oval	44.9	
69. White, purple, star dust	59.4	
70. White, oval	46.5	
INCA BRANCH:		
71. Indigenous, brown mottled + black spots	5.2	Guatemala
72. Indigenous, black	10.0	
73. Black + flecks	68.0	Canal Zone, Panama
74. Flat, star dust, yellow + black flecks	60.0	
75. Flat, star dust, yellow + black flecks	72.4	
76. White, flat, star dust + red-flecked dorsal	70.5	
77. White, flat, star dust, bright red + black flecks	47.3	
78. Very flat, twisted, dark red + black striations	86.0	Guatemala
79. White, very flat, star dust, yellow and black flecks	61.4	Canal Zone, Panama
80. White, very flat, black dorsal, star dust	99.8	
81. White, very flat, purple, star dust, large	81.4	
82. Fordhook, potato, bush, white	108.8	California (commercial varieties)
83. Fordhook, bush, white	107.6	
84. Willow leaf, vine, white	122.0	
85. Lewis, white, vine	134.2	
86. Dreer's Improved Bush, white	106.9	
87. King of the Garden, pole, white	137.6	
88. New Wonder, bush, dull white	166.0	
89. Santa Barbara, speckled, vine	147.6	
90. White, pale, vine	185.9	Ica, Peru
91. White, pale + red spot	193.2	
92. White, pale-purple star dust	161.0	
93. White, pale	218.4	
94. Vega, white, vine	123.0	California (commercial varieties)
95. Pacific, white, vine	134.4	
96. Flynn, white, vine	116.0	


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